THE DEVONIAN GENUS *KEEGA* (ALGAE) REINTERPRETED AS A STROMATOPOROID BASAL LAYER

by ROBERT RIDING

ABSTRACT. The Upper Devonian genus *Keega* Wray, originally described as an alga related to the crustose Corallinaceae, is reinterpreted to be the structurally modified base, here termed basal layer, of a laminar form of the stromatoporoid *Stachyodes* Bargatzky. Besides altering the status of *Keega* and its significance for the phylogeny of crustose coralline algae this conclusion also implies that *Stachyodes* adopted a laminar as well as the more common dendroid form and it supports the view that the primary internal structure of *Stachyodes* is cellular or microreticulate. 'Tubulated' or 'striated' microstructure, common in *Stachyodes*, is regarded as a product of diagenetic alteration. Basal layers are present in at least two other genera of laminar stromatoporoids and are interpreted to be a morphological adaptation facilitating horizontal as well as vertical growth in laminar forms. Type-material of *Keega* is compared with specimens from Alberta, Canada, and *K. australe* is emended and transferred to *Stachyodes*.

CRUSTOSE Corallinaceae range from Jurassic to Recent but have been linked phylogenetically with algal groups originating in the Palaeozoic. Lemoine (1911) suggested that the tribes Lithothamnieae and Lithophylleae were both derived from the Solenoporaceae. This has been restated in evolutionary schemes proposed by Johnson (1960, pp. 62–63) and Wray (1970, fig. 17) which differ in detail but both derive *Lithothamnium* from *Solenopora* during the early Mesozoic and *Lithophyllum* and the articulated Corallinaceae from *Parachaetetes* by way of Upper Palaeozoic genera termed 'ancestral corallines' by Wray. The 'ancestral corallines' differ from the Solenoporaceae in their smaller size, branching habit, and varied internal structure, and they constitute a much less homogeneous group. Most of them have either large-celled tissue (e.g. *Cuneiphycus*) or less distinctly cellular tissue with an apparently fibrous structure (e.g. *Ungdarella*, *Foliophycus*) and lack recognizable reproductive structures. Only two Palaeozoic genera, *Archaeolithophyllum* Johnson from the Carboniferous and *Keega* Wray from the Devonian, have been reported to have the distinct tissue differentiation and reproductive structures which suggest a close affinity with crustose coralline algae.

Wray (1967, p. 16) described *Keega* as having thick coaxial hypothallial tissue, thin perithallial tissue, and single-apertured conceptacles. He compared it with the extant genus *Lithophyllum* Philippi. If this interpretation is correct then *Keega* is not only one of the earliest 'ancestral corallines' but also one of the most advanced structurally. However, doubt has subsequently been cast on the algal nature of *Keega* by Wray and Playford (1970, p. 548) who noted that the supposed perithallial tissue 'is composed of unusually large cells and has a stromatoporoid-like appearance'. They recommended further study of *Keega* but considered it to be a valid taxonomic entity and still tentatively assigned it to the red algae.

Specimens encountered during study of calcareous algae from the Upper Devonian Ancient Wall reef complex in Alberta, Canada, necessitate substantial modification

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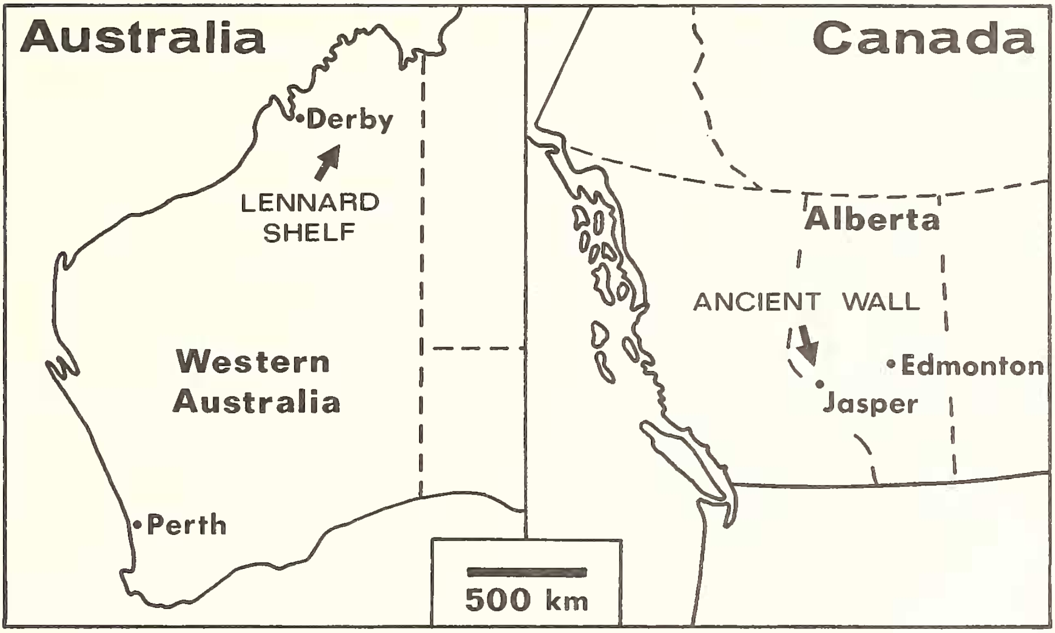
of the original interpretation of *Keega*. They provide evidence that *Keega* is a structural modification, here termed basal layer, of the lower part of a laminar form of the stromatoporoid *Stachyodes* Bargatzky. Examination of type and comparative material of *Keega* from Western Australia supports this conclusion and warrants emendation of *K. australe* and its transfer to *Stachyodes*. This reinterpretation also has significant implications for *Stachyodes*. It suggests that *Stachyodes* adopted a laminar as well as the more common dendroid form and by relating *Keega* and *Stachyodes* it provides evidence to support Lecompte's (1952, 1956) view that the primary microstructure of *Stachyodes* is microreticulate. Production of a basal layer by *Stachyodes* is a hitherto unrecognized feature of stromatoporoids which is also present in at least two other laminar genera.

OCCURRENCE AND MORPHOLOGY OF *KEEGA*

Keega was described from the Upper Devonian of Western Australia (Wray 1967, pp. 16–19) and has since been reported from the Upper Devonian of Alberta, Canada (Wray and Playford 1970; Riding 1972) and Kielce, Poland (Kaźmierczak 1971, p. 21). It occurs in marine carbonate environments usually associated with stromatoporoids, corals, foraminifers, and calcareous algae.

Type Material. The holotype of *K. australe* was not examined for this study. Material which could be borrowed included thin-sections F6162 (hypotype, Wray 1967, pl. 3, fig. 2), 2C, 50A, 290 B.H. and 3266A deposited in the palaeontological collections of the Geological Survey of Western Australia at Perth. These specimens are from the Windjana Limestone (Frasnian and Famennian) of the Lennard Shelf near Derby, Western Australia (text-fig. 1 and Wray 1967, text-fig. 1). Specimen 50A is from the east end of the Windjana Gorge at co-ordinates 280, 280 E., 2809, 700 N. (Wray pers. comm.). The Windjana Limestone has been interpreted as reef facies by Playford and Lowry (1966). The thin sections show partially recrystallized boundstone and grainstone (terminology of Dunham 1962). In the boundstone *Keega* is associated with tabulate corals (*Alveolites*, *Syringoporella*) and with the algal and foraminiferal genera *Epiphyton*, *Girvanella*, *Renalcis*, *Sphaerocodium*, and *Wetheredella*.

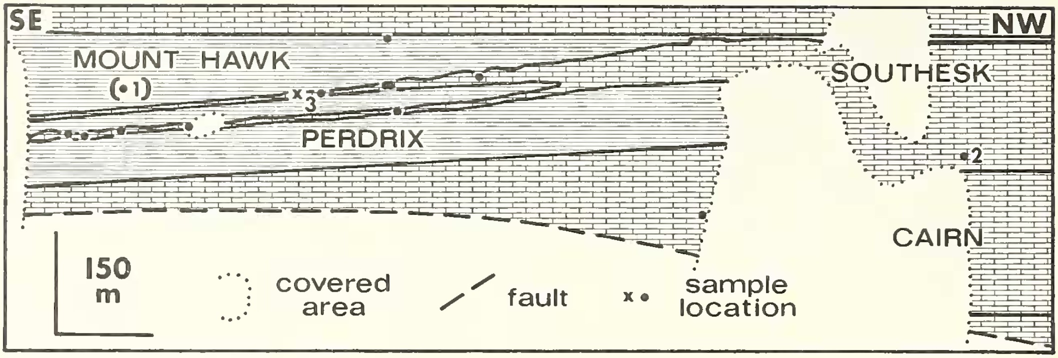
Keega occurs as subhorizontal layers 1–2 mm thick and more than 30 mm long. Scattered branches, rounded in cross-section and up to 8 mm long, extend upward from the main skeleton (Wray 1967, pl. 3, fig. 1). Internally *Keega* consists of numerous crescentic bands of cellular tissue 80–200 μm thick which represent the hypothallus of Wray (pl. 1, fig. 1). These bands are separated by irregular arcs of clear calcite with many short lateral extensions normal to them (Pl. 85, fig. 2). The calcite lacks distinct crystal boundaries. The tissue forming the bands is composed of poorly defined ovoid or rectangular cells 30 by 60 μm in size which are subcircular in cross-section. It includes small irregular patches of clear calcite similar to and often united with those defining the bands. Illustrations of the holotype (Wray 1967, pl. 3, figs. 3, 4) show ovoid areas of sparry calcite up to 500 μm across in the upper part of *Keega*. A short narrow tube extends from each toward the upper surface of the skeleton and Wray interpreted them to be reproductive organs. Of the specimens examined only 50A contains similar structures and they are associated with sinuous tubes, 80–200 μm



TEXT-FIG. 1. Locality maps.

in diameter, which pervade the skeleton (Pl. 85, fig. 3). Specimen F6162 contains traces of tubes, 60–100 μm in diameter (Pl. 85, fig. 2), together with larger circular areas of sparry calcite up to 600 μm across (Pl. 85, fig. 1). Some of these are rimmed by radially fibrous or dense, finely granular calcite. The upper surface of *Keega* is generally a thin layer less than 400 μm thick of brownish calcite similar to the clear calcite patches within the tissue and defining the arcs. It is overlain by sediment or by encrusting *Sphaerocodium* (Pl. 85, fig. 1) and corresponds to the perithallus of Wray. In specimen 3266A this layer is thicker, between 1·00 and 2·25 mm, and has a coarsely reticulate structure with dark ovoid areas 160–200 μm across (Pl. 85, fig. 4). The upper surface of F6162 (Pl. 85, fig. 1) is irregular and it is possible that the specimen is eroded.

Ancient Wall Material. The Ancient Wall reef complex outcrops in the folded and thrust Palaeozoic rocks of the Front Ranges of the Rocky Mountains in south-western Alberta, near the town of Jasper (text-fig. 1). The complex is 50 km across and consists of the Frasnian Cairn and Southesk Formations comprising some 400 m of calcarenites and stromatoporoid biostromes. At the south-eastern margin of the complex at Mount Haultain, a narrow zone of stromatoporoid bioherms marks the edge of the Southesk Formation at the transition to a basinal facies (Perdrix and Mount Hawk Formations). The geological setting is described by Mountjoy (1967). *Keega* is recognizable in thirteen samples from the Cairn, Southesk, and Mount Hawk Formations at Mount Haultain (text-fig. 2). Its apparent localization in the mega-breccias which occur in the lower part of the Mount Hawk Formation adjacent to the biohermal margin of the Southesk Formation is probably due to more intensive sampling of these units. *Keega* occurs in partially dolomitized stromatoporoid



TEXT-FIG. 2. Section showing Frasnian formations at the south-eastern margin of the Ancient Wall reef complex at Mount Haultain, Alberta. Samples marked by dots contain *Keega* (1, G.S.C. 33664; 2, G.S.C. 33665), × indicates ?*Hammatostroma* (3, G.S.C. 33666). Most specimens of *Keega* are from the megabreccias which form tongues in the lower part of the Mount Hawk Formation marginal to the Southesk Formation. Sample 1 is not precisely located but is from the upper megabreccia.

wackestones and boundstones occasionally associated with *Syringoporella* and in packstones and grainstones with crinoids, gastropods, and calcareous foraminifers.

In form and internal structure these specimens of *Keega* are similar to those of the type-material except that they all show upward gradation into a 1·0–3·0 mm thick layer of diffuse calcite crystals with a coarse columnar or reticulate structure (Pl. 85, fig. 5). One specimen (Pl. 86, fig. 1) appears to be a fragment with an eroded margin. The junction between the lower and upper layers is a zone of rapid transition in micro-structure from cellular to diffusely granular. Most specimens contain tubes in the axial part of the lower layer and also in the upper layer although they are less well defined there. The tubes occasionally branch dichotomously and are 100–400 μm in diameter with circular, ovoid, or irregularly rounded cross-sections. They are sub-horizontal in the lower layer and subvertical in the upper although individual tubes do not usually exceed 1 mm in length in any one section. Structures resembling the reproductive organs described by Wray occur in the axial part of the lower layer of a few specimens (Pl. 86, figs. 1, 2).

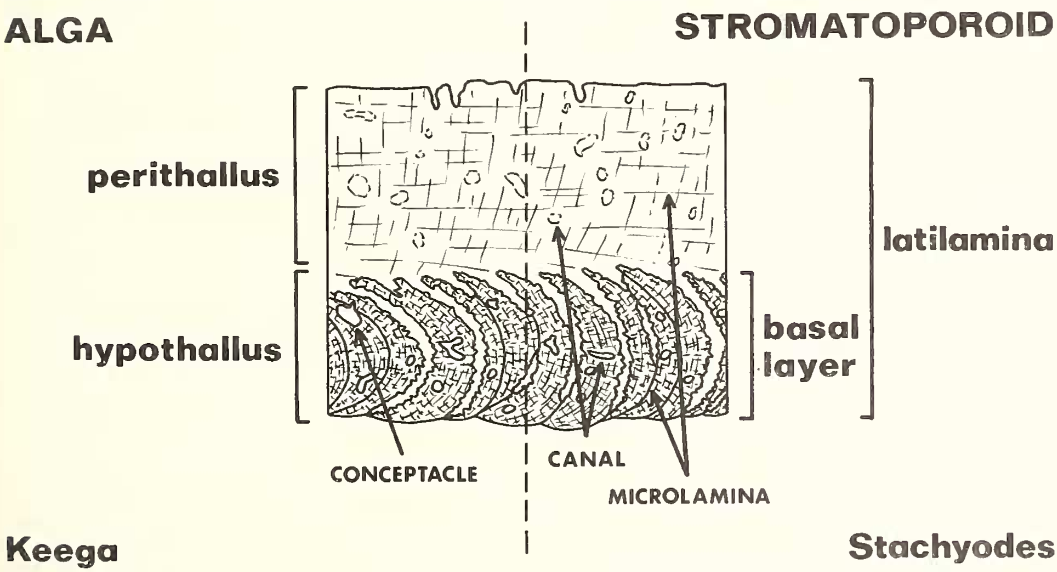
REINTERPRETATION

In most genera of crustose coralline algae the thallus is differentiated into hypothallial and perithallial tissue (see Johnson 1961, pp. 43–45 for a general description of the skeletal structure of crustose corallines). Hypothallial tissue forms the base of flat crusts and the axial part of erect growths. It has large cells commonly arranged in curved or arcuate rows. Perithallial tissue arises from the hypothallial tissue. It has smaller cells usually growing in a regular rectilinear fashion. Flattened circular cavities (conceptacles) containing reproductive structures occur within the peri-thallial tissue.

Although the cellular structure of *Keega* is less well defined than that of crustose Corallinaceae the gross similarity between *Keega* and hypothallial tissue is striking. But *Keega* also exhibits several differences from crustose corallines. The appearance of the upper 'perithallic' layer of *Keega* is, as Wray and Playford (1970, p. 548) noted, stromatoporoid-like. Its diffuse light-coloured lineated microstructure closely resembles that of *Stachyodes*. The cavities scattered through the skeleton lack consistent size, shape, and position. The few which do resemble the conceptacles reported in the holotype appear to be fortuitous sections of the tubes which form a branching network in several specimens from both Western Australia and Alberta. Tubes (or canals) occur in most stromatoporoid genera although their significance is uncertain and comparisons with both sponge canal systems and hydrozoan zooidal tubes have been made. They have no counterpart in coralline algae.

However, the lower (*Keega*) and upper (*Stachyodes*) parts of the specimens have significant structural and microstructural differences which have to be explained if they are to be regarded as parts of the same organism. *Keega* consists of crescentic bands of cellular microstructure and has canals which are subhorizontal in the encrusting specimens. *Stachyodes* commonly has a clear granular, vaguely lineated microstructure and vertical canals.

These differences can be accounted for by regarding *Keega* as the lower structurally modified part (basal layer) of a laminar *Stachyodes* with relatively unaltered microstructure. The upper, typically *Stachyodes*, part of the latilamina has a more regular rectilinear structure with its main elements orientated perpendicular to those of the basal layer and is less resistant to secondary alteration. The light-coloured lineated microstructure often considered typical of *Stachyodes* is strongly altered. Thus the junction between *Keega* and *Stachyodes* corresponds to the top of the basal layer and is a zone of relatively rapid transition in both primary megastructure and in alteration effects on the microstructure. The two aspects of this interpretation, viz. skeletal alteration and development of a basal layer, and their principal implications for *Stachyodes* are discussed in the following section. Algal and stromatoporoidal interpretations of the morphology of *Keega* are contrasted in text-fig. 3.



TEXT-FIG. 3. Diagram contrasting algal and stromatoporoidal interpretations of *Keega*. The original microreticulate microstructure is finely cross-hatched, the altered 'tubulated' microstructure is unshaded.

Specimens which are probably worn, from both Alberta and Australia show that what appear to be laminar forms may be produced by fragmentation and erosion of columnar forms of *Stachyodes* by the removal of one side of the column (Pl. 86, fig. 1) leaving the axial part which has a structure similar to that of the basal layer. However, this interpretation cannot be applied to most of the specimens examined. These lack any sign of erosion (Pl. 85, figs. 3, 4, 5) and thus provide the strongest evidence for the presence of basal layers in indubitably laminar forms.

SYSTEMATIC PALAEONTOLOGY

Gallery, lamina, microlamina, and pillar are used as defined by Galloway (1957, pp. 350–360). Canal refers to the astrorhizal canal of most authors. Terms describing the tissue (solid skeleton) microstructure are defined by Stearn (1966, p. 78). The form and arrangement of the skeletal elements is termed the megastructure (Riding 1974). Specimens from the palaeontological collections of the Geological Survey of Western Australia are prefixed G.S.W.A. Figured specimens from Alberta are deposited in the palaeontological collections of the Geological Survey of Canada (G.S.C.) at Ottawa.

Order STROMATOPOROIDEA Nicholson and Murie, 1878
Family STROMATOPORIDAE Nicholson, 1886
Genus STACHYODES Bargatzky, 1881

Type Species. Stachyodes ramosa Bargatzky, 1881 (placed in synonymy with *Stromatopora* (*Caunopora*) *verticillata* McCoy 1851 by Nicholson 1886, p. 107).

Diagnosis. Tabulate canals with numerous radiating branches which are commonly superposed. Laminae and pillars poorly differentiated; microlaminae thin, dark, intersect tissue at right angles to canals. Tissue microreticulate, commonly altered to granulate calcite with fine lineations paralleling canals.

Description. The solid skeleton constitutes the major part of the coenosteum which may be dendroid, fasciculate, massive, or laminar. Internal cavities are restricted to a distinctive canal system. The canals are crossed by straight, bent, or vesiculose tabulae. The original tissue is cellular or microreticulate, formed by rectangular or subspherical 'cells' with dimensions of 30–55 by 60–150 μm orientated with their long axes parallel to the canals. The microlaminae are distinct non-cellular layers normal to the canals. Enlargement and coalescence of calcite grains commonly destroys this microstructure to produce a mass of granular pale-brown calcite which lacks distinctive structures but retains vague discontinuous lineations, poor microlaminae, and scattered speckled patches of fine-grained grey calcite. The lineations are arranged radially in cross-sections and longitudinally in axial sections. They are normal to the microlaminae and correspond to the vertical lines of the original microstructure.

Discussion. Recognition of a laminar form of *Stachyodes* supports Lecompte's (1956, p. F126) removal of the genus from the purely dendroid stromatoporoids comprising the Idiostromatidae of Nicholson (1886, p. 74). Paucity of internal spaces in *Stachyodes* makes distinction between laminae and pillars difficult. The galleries described by some authors are more aptly termed horizontal canals. The resulting poorly differentiated skeletal structure has been termed reticulated (Nicholson 1886, pp. 34, 107; Lecompte 1952, p. 259; 1956, p. F113) or amalgamated (Galloway 1957, p. 350). Distinct thin lines within the solid skeleton were noted by Galloway (1957, p. 445) when he described *Stachyodes* as 'composed of thick laminae which are separated by thin dark lines'. He went on to suppose that 'the laminae themselves represent the interlaminar spaces of most stromatoporoids'. Whether or not interlaminar spaces (galleries) become filled in some stromatoporoids it is confusing to then term them laminae. In contrast, Lecompte (1952, p. 298; 1956, p. F136) apparently regarded the dark lines themselves as laminae. This usage is also inappropriate since lamina in stromatoporoids usually denotes a tabular skeletal element joined by pillars and enclosing galleries, whereas the dark lines in *Stachyodes* are usually separated by hard tissue. Since they are comparable with the dark microlaminae present in some species of *Stromatopora* (Stearn 1966, p. 111 and pl. 17, fig. 7) this term is used for them here.

Secondary alteration of the tissue of *Stachyodes* is indicated by the transition from a distinct cellular or microreticulate microstructure to a poorly defined lineated microstructure. The lineations, also termed striae by Lecompte (1956, p. F136), were interpreted to be tubules by Nicholson (1886, pp. 107–108) and subsequently a tubulate or porous microstructure has commonly been regarded as diagnostic of *Stachyodes* (Galloway 1957, p. 440; Yavorsky 1957, p. 58). However, in well-preserved material (especially of *S. caespitosa* and *S. paralleloporoides*) from Belgium Lecompte (1952, p. 301) noted that the fine black lines representing the tubules of Nicholson are crossed at right-angles by similar but less well-preserved ones. He compared the resulting microreticulate microstructure with that of *Parallelopora ostiolata* and expressed the view that the microstructure of *Stachyodes* is 'essentially microreticulate' (1952, p. 298; 1956, p. F113). The tubules have since been described by Stearn (1966, p. 117) as 'rod-like concentrations (15 μm in diam.) of dark specks (1 μm across)'. Lecompte (1952, p. 301) alluded to, but did not pursue, the idea that microstructural variation in *Stachyodes* is due to diagenetic effects. The microstructure of *Stachyodes* in specimens of *S. costulata* Lecompte, *S. crebrum* Stearn, *S. spongiosum* Stearn, and *S. thomasclarki* Stearn examined from several Devonian areas of western Canada is a mass of poorly developed, irregularly sized calcite grains which contrast with the clear distinct crystals occupying the canals. *Stachyodes* referred to as *Keega* provides a link between this altered microstructure and the original one identified by Lecompte by showing them in juxtaposition: the former in the upper part of the latilamina and the latter in the lower part. Preferential preservation of the lower part of the latilamina is an unexplained but characteristic feature of stromatoporoid alteration (Riding 1974) which appears to be independent of the occurrence of a basal layer. The transition between the two microstructures is effected by enlargement and coalescence of calcite grains which merge with and enclose the original microreticulate tissue until only vague patches and lines of it remain as poor microlaminae and as the aligned specks of the 'tubules'. The degree of alteration commonly affecting *Stachyodes* corresponds to the advanced to extreme stages in the scheme of progressive alteration of stromatoporoids proposed by Riding (1974).

Interest in skeletal alteration in stromatoporoids has focused mainly on evaluating the usefulness of microstructural criteria for taxonomy. Whether failure to recognize moderate alteration has led to the erection of poorly delimited or overlapping taxa is not yet clear, but *Syringostroma*? *confertum* Stearn is an example of confusion caused by more advanced alteration. Converging alteration effects upon species belonging to several stromatoporoid genera was one of several hypotheses suggested by Stearn (1967, p. 800) to explain the nature of *S.*? *confertum* and has been borne out subsequently (Birkhead and Murray 1970; Stearn 1972, p. 375). Thus, transferral of *Stachyodes costulata* Lecompte to *Syringostroma*? by Fischbuch (1970, p. 1079) was based on secondary rather than original similarities in skeletal structure. Fischbuch's illustration (pl. 148, fig. 6) shows the central part of the column with relatively unaltered microreticulate structure grading outwards into an altered marginal zone.

Stachyodes australe (Wray 1967)

Plate 85, figs. 1-5

1967 *Keega australe* Wray, p. 18, pl. 3, figs. 1-6; text-fig. 6.

Diagnosis. Thin laminar *Stachyodes* with basal layer exhibiting subhorizontal canals and arcuate microlaminae normal to them.

Description. Laminar stromatoporoid usually less than 4 mm thick with rare rounded branches up to 2 mm in diameter and 8 mm long rising from the laminar coenosteum. Basal layer commonly well developed and constituting up to one-third of the thickness of the latilamina. Canals subhorizontal in basal layer, curving upward to become vertical. Tissue microreticulate or cellular. Microlaminae prominent, normal to canals; subvertically arcuate in basal layer, horizontal above. Tissue above basal layer commonly altered to indistinct grains of brownish calcite, rarely preserving the original microstructure but retaining the canals.

Discussion. The original description of this species was almost entirely restricted to the basal layer. It is emended here to include the thicker upper part of the latilamina with more regular structure and common alteration. The concept of distinct structural modification of the lower part of the stromatoporoid latilamina is new. The term *basal layer* is introduced for this zone, defined as: the structurally modified basal part of a latilamina characterized by bending or folding, often arcuate, of the laminae

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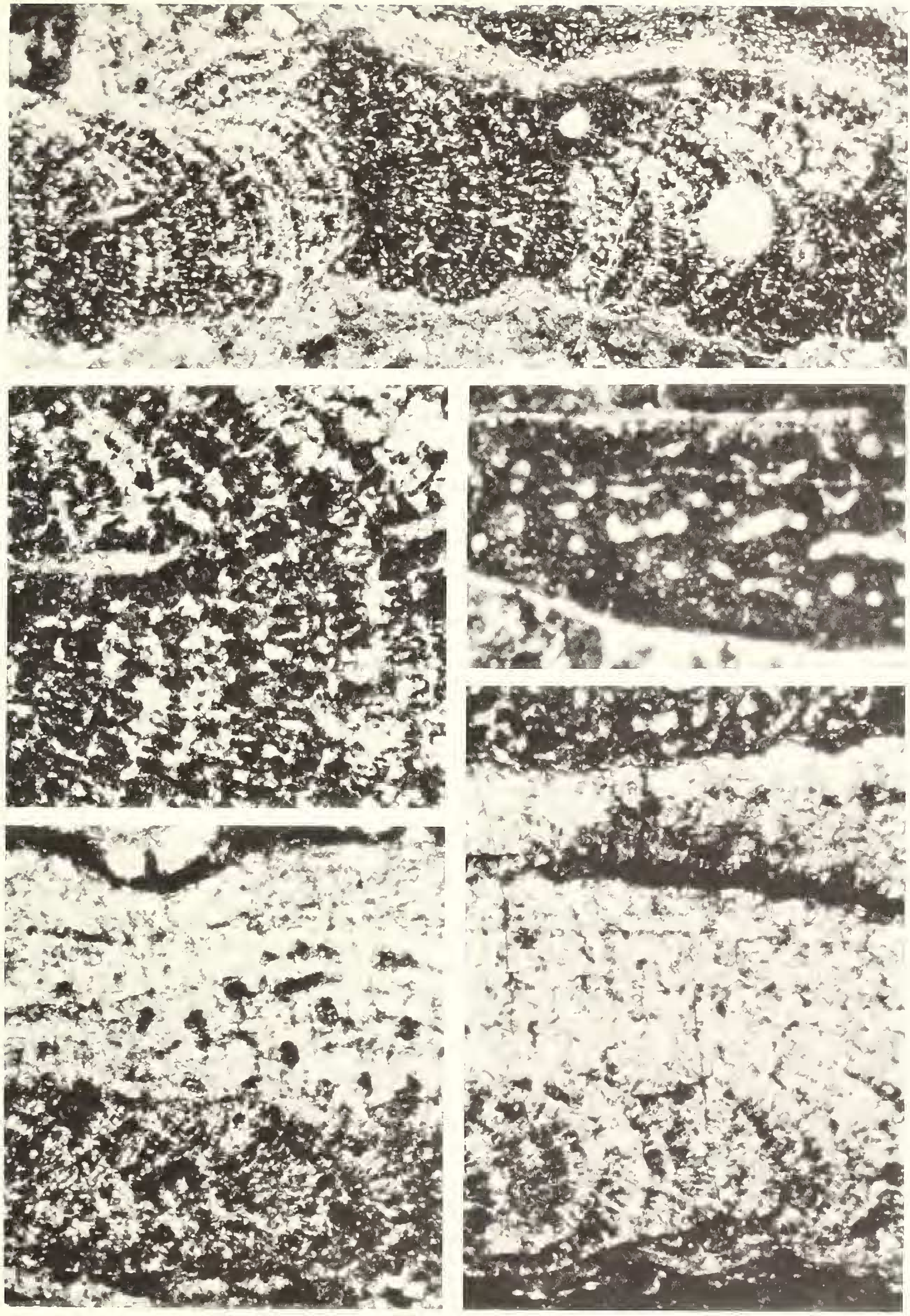
EXPLANATION OF PLATE 85

Stachyodes australe (Wray), longitudinal sections except fig. 3.

Figs. 1, 2, 3, 4. Specimens from the Upper Devonian of the Lennard Shelf, Western Australia. 1, G.S.W.A. F6162, hypotype, Windjana Limestone, Windjana Gorge; showing crescentic bands of cellular or microreticulate tissue and thin upper layer of clear calcite; *Sphaerocodium* encrusts upper surface at top right which may be eroded, ×20. 2, detail of 1 showing microstructure and arcs of clear calcite penetrated by a small horizontal canal on the left, ×50. 3, G.S.W.A. 50A, Windjana Limestone, Windjana Gorge; showing sinuous canals and thin upper layer of clear calcite; the section is transverse to the microstructure which appears as a mosaic of small 'cells', ×20. 4, G.S.W.A. 3266A, Windjana Limestone, 37 km north-east of Christmas Creek; showing thick band of relatively clear altered calcite above basal layer, ×20.

Fig. 5. G.S.C. 33664, Mount Hawk Formation (Frasnian), Mount Haultain, Alberta; basal layer grades upward into clear calcite with a vague reticulate structure overlain by a second latilamina lacking a recognizable basal layer; this is overlain in turn by a different stromatoporoid genus (top), ×20.



1 2 3 4 5

RIDING, *Stromatoporoids*

and microlaminae and subhorizontality of the canals; the pillars and laminae may be thickened and the lower surface is commonly irregular. In *Stachyodes australe* the basal layer has subhorizontal canals and arcuate microlaminae normal to them; its development is variable (Pl. 85, fig. 5).

Dendroid forms of *Stachyodes* commonly have a zone with arched microlaminae in the inner part of the column (e.g. *S. costulata*, Lecompte 1952, pl. 65, fig. 1*b*; Fischbuch 1970, pl. 148, fig. 7). In eroded specimens (Pl. 86, fig. 1) this axial zone may be confused with the basal layer with which it is very similar and probably related. The presence of both basal layers and axial zones in *Stachyodes* emphasizes the broad similarity between these structural modifications of stromatoporoids and the hypothallial tissue of crustose Corallinaceae. Basal layers are also present in specimens of ?*Hammatostroma* and to a lesser extent in *Actinostroma* (see Lecompte 1956, fig. 92, 2, the specimen is apparently inverted). In ?*Hammatostroma* (Pl. 86, fig. 4) the basal layer shows arcuate laminae which have pillars radiating subhorizontally from them forming large crescents whose tips protrude into the underlying cavity.

Parks (1935, p. 28), arguing in favour of a foraminiferal affinity for stromatoporoids, noted 'the occurrence in many stromatoporoids of a basal layer of chambers quite different from those of the general test. In some species this layer occurs at the base of each latilamina.' No illustrations of the layer were given but this description corresponds well with that of the basal layer as it is defined here. A structure called the epitheca, also termed peritheca and holotheca, has been described as 'a thin, wrinkled, basal layer, of finer and different structure than the superjacent normal structures' occurring at the base of many stromatoporoid coenostea (Galloway and St. Jean 1957, p. 40; Galloway 1957, p. 387). It does not appear to be comparable with the basal layer described here.

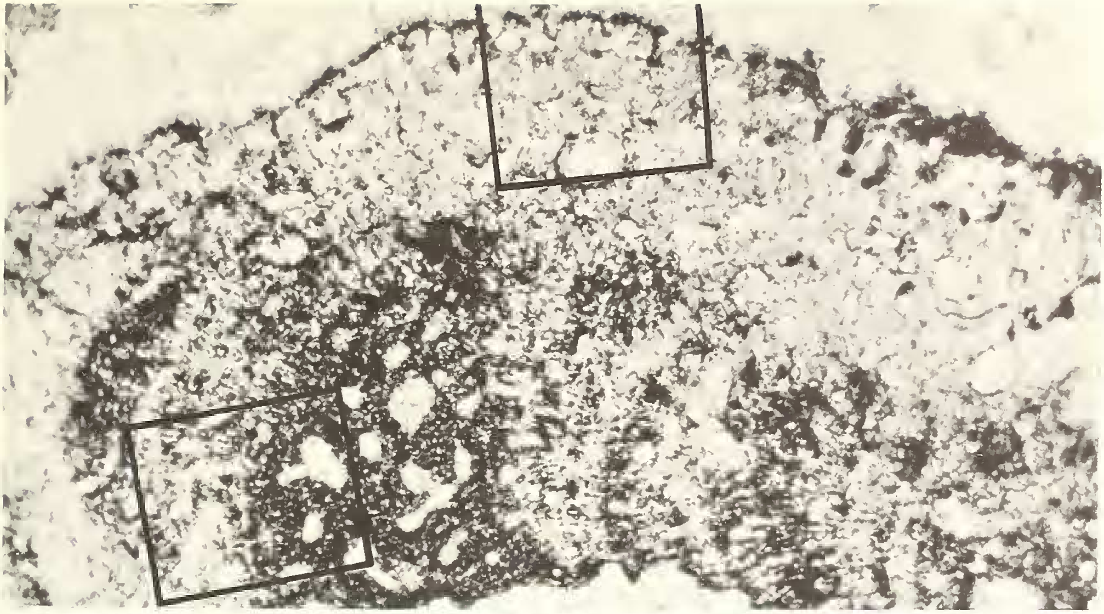
The origin of basal layers may be linked with a colonizing function. Their curved laminae and microlaminae would have had potential for horizontal as well as vertical growth so that they could spread laterally over new substrates and even overgrow small cavities (Pl. 86, fig. 4). Secondary tissue arose perpendicularly to the basal layer and is the more regular tissue usually dealt with in systematic descriptions. Variable development of the basal layer is not readily explained, although it is probably related to differing modes of propogation in stromatoporoids about which very little is known. Some support for this idea is shown by the more common occurrence of basal layers in latilaminae which overlie sediment or cavity than in those resting upon stromatoporoids of the same species.

EXPLANATION OF PLATE 86

Stromatoporoids from the Upper Devonian, Mount Haultain, Alberta; longitudinal sections.

Figs. 1, 2, 3. *Stachyodes* sp., G.S.C. 33665; Southesk Formation (Frasnian). 1, showing basal layer or axial zone and upper altered zone with canals opening on to upper surface; fragment with probably eroded lower margin, ×20. 2, detail of basal layer or axial zone showing branching canal resembling a conceptacle, ×50. 3, detail of altered zone contrasting speckly microstructure with distinct calcite crystals filling canal at bottom centre; ×50.

Fig. 4. ?*Hammatostroma* sp., G.S.C. 33666; Mount Hawk Formation (Frasnian); showing basal layer with crescentic laminae and sub-horizontal pillars overgrowing a cement-filled cavity; upper part of latilamina is altered (see Riding 1974), ×20.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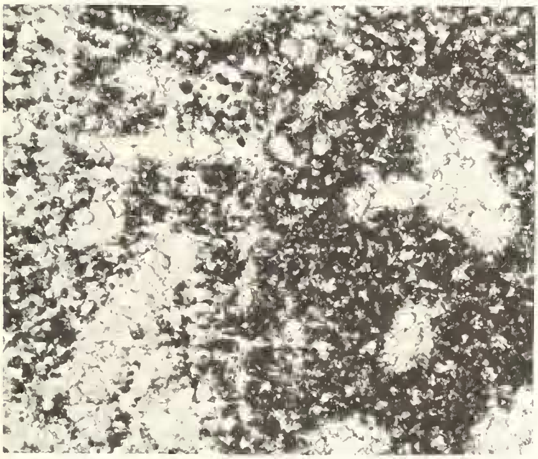
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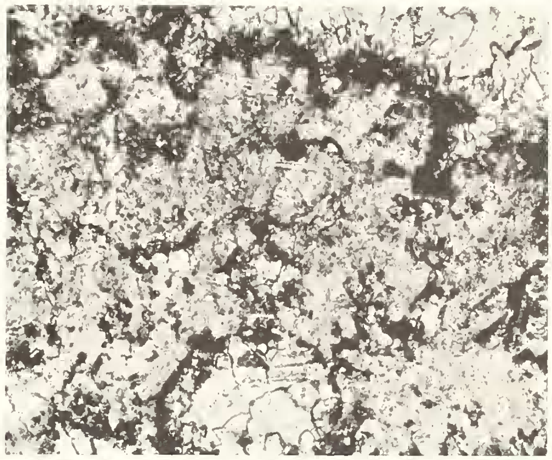
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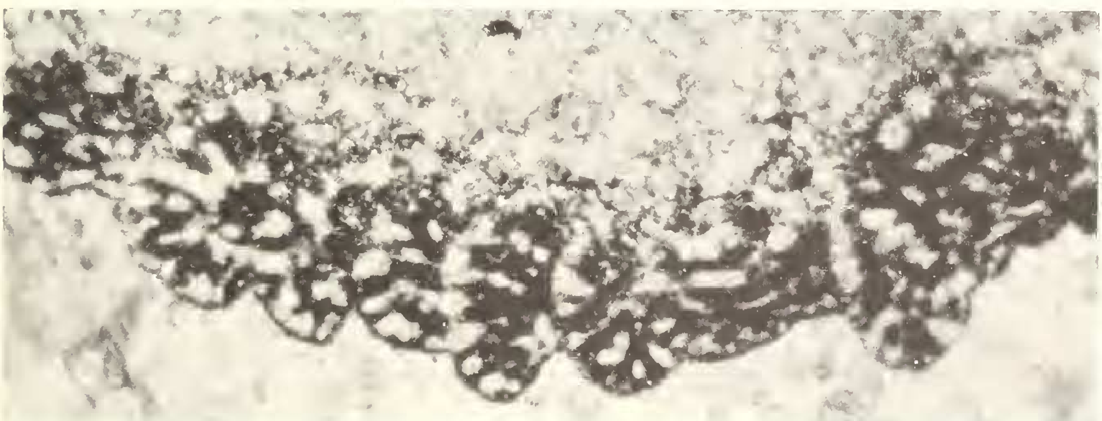
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CONCLUSIONS

Study of *Keega* highlights several aspects of the structure of stromatoporoids and the fossil record of the crustose Corallinaceae. Although *Keega* superficially resembles the hypothallial tissue of certain crustose Corallinaceae and was for this reason originally placed in the Rhodophyta it possesses canals and grades vertically into tissue characteristic of *Stachyodes*. Megastructural and microstructural differences between the lower and upper parts of latilaminae showing this gradation are due to both primary differences in megastructure and to subsequent alteration of the microstructure. The significance of these observations can be summarized as follows:

1. Most species of *Stachyodes* have a dendroid external form but at least one laminar species, *S. australe* (Wray), can be recognized.
2. *S. australe* has a structurally modified zone with arcuate microlaminae and horizontal canals at the base of the latilamina which is termed the basal layer. The upper part of the latilamina has horizontal microlaminae and vertical canals.
3. Dendroid forms of *Stachyodes* commonly have an axial zone which resembles the basal layer in structure but which is surrounded by 'normal' skeletal structure with microlaminae parallel to the axis of the column. It is suggested that the axial zone and basal layer are closely related and that they are analogous with the hypothallial tissue of crustose Corallinaceae.
4. Basal layers also occur in ?*Hammatostroma* and *Actinostroma*. They are suggested to be a response to the need for horizontal as well as vertical growth during colonization of a new substrate by the stromatoporoid.
5. The skeleton of *Stachyodes* is often diagenetically altered to a mass of brownish, poorly formed calcite grains. This 'tubulated' or 'striated' microstructure has generally been regarded as diagnostic of the genus. However, well-preserved specimens show original microreticulate microstructure especially in the basal layer and the axial zone.
6. The basal layer of *S. australe*, together with a thin upper layer of 'normal' but altered structure was originally described as *Keega australe* Wray and considered to belong to the Rhodophyta because of its resemblance to the hypothallial tissue of crustose Corallinaceae. The nature of *K. australe* as essentially a basal layer rather than a complete latilamina necessitates emendation of the species as well as its reassignment to *Stachyodes*.
7. Recognition that this species is not an alga removes what was assumed to be one of the earliest and most advanced Palaeozoic ancestors of the crustose Corallinaceae.

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